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Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming

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Although seedlings of *Abies lasiocarpa* are generally more abundant than those of *Picea engelmannii* in the understory of mature spruce–fir forests throughout the central and northern Rocky Mountains, little information exists concerning environmental or plant factors that may influence the establishment of these two conifers. Field measurements in the Medicine Bow Mountains of southeast Wyoming showed that seedlings of *A. lasiocarpa* had greater photosynthetic rates at low understory light levels and required lower levels of incident radiation for saturation of photosynthesis compared with those of *P. engelmannii*. However, both conifers occurred in understory locations where total daily solar radiation was equally low (<2 $MJ \cdot m^{-2} \cdot day^{-1}$) and thus, a lack of light did not appear to be responsible for the low number of *P. engelmannii* seedlings in the understory. In contrast, seedlings of *P. engelmannii* were substantially more abundant at locations with thinner litter layers compared with those of *A. lasiocarpa*. Also, laboratory studies showed that the smaller seeds of *P. engelmannii* germinated more rapidly and at lower temperatures than seeds of *A. lasiocarpa* although growth of tap roots on *A. lasiocarpa* seedlings was greater initially ($\simeq$ 200% longer in 2-week-old seedlings) as well as for 10-week-old seedlings (50% longer). The deeper penetrating tap root of *A. lasiocarpa* seedlings may enable this conifer to establish more abundantly on thick, rapidly drying litter layers that are characteristic of mature spruce–fir forests. In contrast, establishment of *P. engelmannii* seedlings may be limited to microsites without a thick litter layer such as disturbed areas or decomposing wood, where surface drying may occur more gradually throughout the summer. These results are discussed in terms of the potential effects of seedling establishment on the observed patterns in climax vegetation of central and northern Rocky Mountain subalpine forests.

Introduction

In the central and northern Rocky Mountains, seedlings of subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) are often more numerous than those of Engelmann spruce (*Picea engelmannii* Parry) in the understory of mature spruce–fir forests (Hodson and Foster 1910; Oosting and Reed 1952; Smith 1955; Day 1964, 1972; Miller 1970; Loope and Gruell 1973; Schmid and Hinds 1974; Whipple and Dix 1979). In fact, Day (1972) and Wirsing and Alexander (1975) have suggested that if existing spruce–fir forests remained disturbance-free for an adequate period of time, *A. lasiocarpa* would be the climax conifer at many sites in the subalpine zone. However, other investigators have felt that *P. engelmannii* and *A. lasiocarpa* may co-occur indefinitely, despite the greater number of *A. lasiocarpa* seedlings. This continuing co-occurrence could result from the greater longevity of *P. engelmannii* trees (Oosting and Reed 1952), the effects of cyclic insect outbreaks on stand structure (Schmid and Hinds 1974), or the periodic recruitment of *P. engelmannii* seedlings (Miller 1970; Whipple and Dix 1979).

Specific plant and environmental factors influencing the establishment of western conifers in understory environments have received little attention. Three hypotheses which have been proposed previously to explain the greater number of *A. lasiocarpa* seedlings relative to *P. engelmannii* are (*i*) the inability of *P. engelmannii* to utilize the low levels of solar radiation in a subalpine understory (Baker 1949; LeBarron and Jemison 1953; Krajina 1965; Miller 1970; Day 1972; Loope and Gruell 1973; Alexander 1974; Whipple and Dix 1979), (*ii*) greater success in establishment of *A. lasiocarpa* seedlings owing to more rapid seedling growth from the larger seeds of *A. lasiocarpa* (Hodson and Foster 1910; Oosting and Reed 1952; Smith 1954, 1955; Smith and Clark 1960; Day 1964), and (*iii*) greater mortality of *P. engelmannii* seeds and seedlings compared with those of *A. lasiocarpa*, caused by pathogenic agents in the forest floor of mature spruce–fir forests. However, the results of Daniel and Schmidt (1972) did not support the latter hypothesis. A fourth hypothesis invokes a differential susceptibility to desiccation that could occur with different substrates or litter depths.

The purpose of this study was to investigate the first two hypotheses listed above. To evaluate the initial hypothesis, the location of seedlings in the understory in relation to understory light, and their photosynthetic responses to low light levels was measured. The second hypothesis was evaluated using measurements of seed germination, early seedling growth, and the location of

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seedlings in relation to understory litter depths to determine if differences in seedling development between *P. engelmannii* and *A. lasiocarpa* could contribute to the observed differences in establishment of these conifers. The relative importance of each of these factors is discussed in relation to seedling patterns in the understory and the observed vegetation patterns of subalpine conifers in the central and northern Rocky Mountains.

Materials and methods

Study sites

Study sites were located in a virgin spruce–fir forest in the Snowy Range Natural Area (3100 m) of the Medicine Bow National Forest approximately 65 km west of Laramie, Wyoming (41°21′ N, 106°14′ W). Two study areas (0.2 and 0.1 ha) were chosen in stands with different age structure to evaluate the relationships between the understory location of *P. engelmannii* and *A. lasiocarpa* seedlings and the corresponding incident solar radiation and litter depth at each seedling location. Seedlings (<30 cm tall) were sampled in both study areas along with the density of saplings (>30 cm tall to 10 cm diameter at breast height (dbh)) and the density and basal area of trees (>10 cm dbh) using a point-quarter distance sampling method (Cottam and Curtis 1956). Estimates of the area of the forest floor occupied by different seedbeds (i.e., litter, decayed wood, moss etc.) were made using a line intercept method (Mueller-Dombois and Ellenberg 1974). Ages of the largest trees at each site were estimated from the relationship between diameter and age described in Oosting and Reed (1952) for adjacent virgin stands.

Understory light and photosynthesis

All seedlings in both study areas were marked and 137 (38% of the total) were chosen randomly for measurements of the total daily solar radiation received at each seedling location. Incident photosynthetically active radiation (PAR, 0.4–0.7 μm) was measured at 0.5-h intervals from dawn to dusk at each seedling location over 4 clear days in late June. At each location, the surface of the PAR sensor was positioned perpendicular to the vertical axis of the seedling and directly above the terminal leader. The type of seedbed and the depth of the litter layer (organic matter above mineral soil) were also determined at each seedling location. Incident PAR was measured with a light meter (Lambda instruments model LI-185A) and a quantum sensor (LI-190S) and converted to total solar radiation using an empirical relationship developed with a radiometer (Eppley model PSP). The frequency distribution of the two conifers relative to total solar radiation was tested for normality using a chi-square analysis (Zar 1974).

The photosynthetic responses of *P. engelmannii* and *A. lasiocarpa* seedlings to low incident PAR were compared under natural understory conditions for six 2- to 4-year-old seedlings of each conifer species. Net photosynthesis per unit leaf area (J_{CO_2}) and the amount of incident PAR at photosynthetic saturation (95% of maximum J_{CO_2}) and compensation ($J_{CO_2} = 0$) were determined for undisturbed seedlings sealed in a Plexiglas cuvette (equipped with a fan) coupled to an open-flow infrared gas analyzer (Beckman model 865). All seedlings of each species were watered daily for 3 days before photosynthesis measurements began and were at natural locations that were receiving approximately equal amounts of total daily solar radiation. The amount of light striking the seedling during photosynthetic measurements was regulated with a variable auto-transformer (Powerstat model 3PN116B) connected to a 150 W tungsten-filament flood lamp filtered through 10 cm of water. The quantity of light incident on the seedlings was measured with the Lambda light sensor and leaf temperatures were measured with a fine wire (0.018 cm diameter) copper–constantan thermocouple wrapped around an unshaded needle near the middle of the seedling. Leaf temperatures were maintained at 20–23°C for all light response curves. Total leaf area was determined geometrically using a light microscope and dial calipers, and J_{CO_2} was expressed on a projected leaf area basis (1/2 total leaf area).

Seed size, germination, and seedling growth

The influence of seed size, germination, and early seedling growth on seedling establishment in the understory was evaluated using seeds obtained from mature cones collected in north central Colorado and southeast Wyoming during autumn 1980. Seeds were grouped into lots of 100 and weighed (± 0.1 mg) before storage at 4°C until germination studies were initiated. Prior to the germination studies, six to eight replicates of 50 seeds of each species were surface sterilized in a 0.3% solution of calcium hypochlorite for 5 min and rinsed 3 times in distilled water. The seeds were placed on the surface of an agar medium (1%) in sterile petri dishes and placed in an environmental chamber at temperatures of 10, 15, 20, and 25°C with an 8-h photoperiod. Germinated seeds were counted and removed daily and germination was considered complete when the radicle protruded at least 1 mm.

Seedling growth was monitored over a 10-week period under greenhouse conditions which included a 14-h photoperiod with mean day air temperatures of 19°C (15–22°C range), mean night temperatures of 13°C (10–15°C), total daily radiation typically between 4.0–5.5 $MJ \cdot m^{-2} \cdot day^{-1}$, and relative humidity averaging 30% (12–53%). These growth conditions are similar to those reported during midsummer by Young and Smith (1979, 1980) and Smith (1981) for the subalpine understory environment of the Medicine Bow Mountains. Germinated seeds were transferred from the petri dishes along with a small agar block to 15 cm deep pots containing sand. Each pot contained five to seven seedlings of either *P. engelmannii* or *A. lasiocarpa* and was watered daily and fertilized weekly with a commercial fertilizer (Ra-Pid-Gro Corp., Dansville, NY). Seedlings were harvested weekly by randomly selecting one pot of each species and systematically rearranging the remaining pots. Harvested seedlings were carefully removed from the soil, washed, and root and shoot lengths were measured (±1 mm). Root and shoot dry weights were then determined (±0.1 mg) after oven-drying at 85°C for 24 h. Relative growth rates (RGR) were calculated from dry weight measurements using the equation (Evans 1972);

$$[1] \quad \mathrm{RGR} = \frac{\ln W_{t_2} - \ln W_{t_1}}{t_2 - t_1}$$

where W is total dry weight at times t_1 and t_2. Statistical comparisons of sample means for all measurements were made using Student's *t*-test (Zar 1974).

TABLE 1. Overstory and understory stand characteristics for the principal conifers at the two study sites

Stand	Total density (trees/ha)	Density (trees/ha)	Relative density (%)	Average basal area (cm^2)	Basal area (m^2/ha)	Relative basal area (%)
Science camp						
Mature trees						
(>10 cm dbh)	921(±59)					
Picea engelmannii		678	74	932	63	89
Abies lasiocarpa		230	25	302	7	10
Pinus contorta		13	1	829	1	1
Saplings						
(< 10 cm dbh)	2217(±194)					
P. engelmannii		431	19	—	—	—
A. lasiocarpa		1786	81	—	—	—
P. contorta		—	—	—	—	—
Seedlings						
(< 30 cm tall)	1789					
P. engelmannii		726	41	—	—	—
A. lasiocarpa		1063	59	—	—	—
P. contorta		—	—	—	—	—
Natural area						
Mature Trees	728(±46)					
P. engelmannii		394	54	1671	66	86
A. lasiocarpa		334	46	323	11	14
Saplings	938(±65)					
P. engelmannii		195	21	—	—	—
A. lasiocarpa		743	79	—	—	—
Seedlings	1027					
P. engelmannii		254	25	—	—	—
A. lasiocarpa		773	75	—	—	—

NOTE: Values in parentheses represent one standard error of the mean. *Pinus contorta* is ssp. *latifolia* (Engelm.).

Results

Although trees of *P. engelmannii* were more abundant and had greater basal area in the overstory than those of *A. lasiocarpa* at both study sites, saplings and seedlings of *A. lasiocarpa* were more numerous in the understory (Table 1). The estimated age of the oldest trees at the Natural Area site (420 year) was greater than for trees at the Science Camp site (340 year) even though both sites were within a continuous spruce–fir forest. Also, the ratio of seedlings of *A. lasiocarpa* to *P. engelmannii* was greater at the Natural Area site (≅3:1) than at the Science Camp site (≅1.5:1).

Understory light, photosynthesis, and litter depth

The distribution of seedlings according to the total daily solar radiation received at each seedling location was similar at both sites and therefore combined (Fig. 1). The mean total daily radiation received by *P. engelmannii* seedlings was 6.6 $MJ \cdot m^{-2} \cdot day^{-1}$ compared with 5.6 $MJ \cdot m^{-2} \cdot day^{-1}$ for those of *A. lasiocarpa* ($P < 0.05$). The chi-square analysis indicated that neither species deviated significantly from a normal distribution relative to total daily radiation received. Seedlings of both species occurred in locations receiving total daily radiation ranging from < 2.0 to > 13.0 $MJ \cdot m^{-2} \cdot day^{-1}$; however, the frequency of *A. lasiocarpa* seedlings decreased more uniformly as solar radiation increased compared with those of *P. engelmannii* (Fig. 1). The greatest proportion of the total daily solar radiation (62%) was received by seedlings of both conifers at midday (solar noon ± 2 h) and *A. lasiocarpa* seedlings occurred more frequently at locations receiving less midday radiation compared with *P. engelmannii* seedlings which were more abundant at locations receiving greater midday radiation (Fig. 1).

A comparison of the influence of light level on J_{CO_2} for seedlings of both conifers indicated that net photosynthesis was greater in *A. lasiocarpa* seedlings at all light levels (Fig. 2) with an approximately 34% greater mean maximum J_{CO_2} for *A. lasiocarpa* (1.72 $\mu mol \cdot m^{-2} \cdot s^{-1}$), compared with *P. engelmannii* (1.28 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Net photosynthesis became saturated at light levels of near 780 $\mu E \cdot m^{-2} \cdot s^{-1}$ in *A. lasiocarpa* compared with 1060 $\mu E \cdot m^{-2} \cdot s^{-1}$ for *P. engelmannii* while light compensation points ranged between 60 and 70 $\mu E \cdot m^{-2} \cdot s^{-1}$ for both conifers.

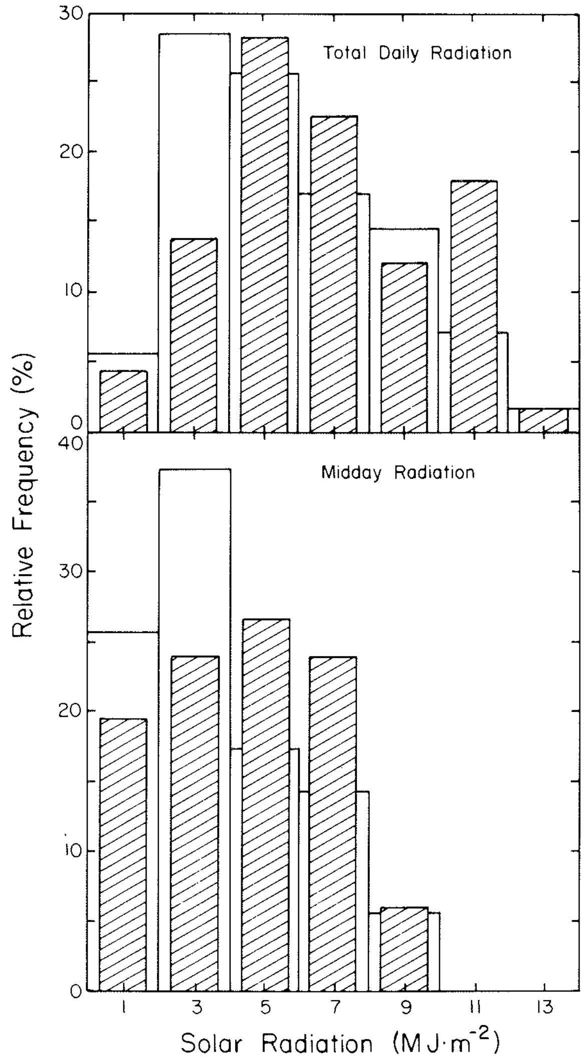

FIG. 1. Relative frequency of *A. lasiocarpa* and *P. engelmannii* seedlings at understory locations according to the quantity of solar radiation received integrated over the entire day and the midday period (solar noon ± 2 h). Data are combined for the two study sites. Hatched bars represent *P. engelmannii*, open bars *A. lasiocarpa*.

Seedlings of *P. engelmannii* were located in areas where the litter layer above mineral soil was significantly thinner compared with locations with *A. lasiocarpa* seedlings ($\bar{x}$ = 1.9 cm vs. 3.3 cm, $P < 0.05$). Moreover, only 5% of the *P. engelmannii* seedlings were located in litter > 2.5 cm deep compared with 42% for *A. lasiocarpa* (Fig. 3). Also, 19% of the *P. engelmannii* seedlings and 15% of the *A. lasiocarpa* seedlings were found growing on decomposing wood which occupied < 5% of the forest floor.

Seed size, germination, and seedling growth

Seed weight, germination success, and early seedling growth were measured to quantify differences between *A. lasiocarpa* and *P. engelmannii* that may influence seedling establishment in the subalpine understory environment. Although seeds of *A. lasiocarpa* averaged 175% heavier than seeds of *P. engelmannii* ($\bar{x}$ = 7.9 mg vs. 2.9 mg, $P < 0.01$), the lighter seeds of *P. engelmannii* germinated earlier and more rapidly at all temperature treatments (Table 2). Fifty percent of the maximum germination recorded at each temperature occurred at about 7 days after planting for *P. engelmannii* compared with about 15 days for *A. lasiocarpa*. Maximum germination was slightly greater for *P. engelmannii* (54.8%) than *A. lasiocarpa* (46.0%) and germination was reduced from maximum values by about 84% at 15°C ($P < 0.05$) and 98% at 10°C ($P < 0.05$) in *A. lasiocarpa* compared with 26% (not significant) and 93% ($P < 0.05$), respectively, in *P. engelmannii*.

For seedlings grown under controlled greenhouse conditions, no significant difference in shoot length was recorded between *A. lasiocarpa* and *P. engelmannii* throughout the 10 week growth period (Fig. 4). The decrease in shoot length from the 2nd to the 3rd week was probably caused by the loss of the seed coat and expansion of the cotyledons. Shoot lengths did not increase significantly after the 3rd week, even though primary needles developed in both conifers when seedlings were 4 weeks old. However, 2 weeks after germination the mean length of the tap root in *A. lasiocarpa* seedlings was over 200% greater than the length of the tap root in *P. engelmannii* seedlings (29.0 mm vs. 9.4 mm) (Fig. 4). The difference in mean length of tap root increased to 35.1 mm at 10 weeks. Throughout the study, length of tap root was synonymous with the depth of penetration of the tap root. The average rate of root elongation calculated for the entire 10-week period was 1.77 mm·day^{-1} for *A. lasiocarpa* and 1.27 mm·day^{-1} for *P. engelmannii*. The maximum length of tap root recorded was 171 mm for *A. lasiocarpa* compared with 129 mm for *P. engelmannii*. Lateral roots developed in both conifers at 5 weeks, but were more numerous and longer at the end of the study in *P. engelmannii*. Root weights were generally greater for seedlings of *A. lasiocarpa* than those of *P. engelmannii* and the mean root weight of 10-week-old seedlings was 10.7 mg for *A. lasiocarpa* compared with 7.0 mg ($P < 0.01$) for *P. engelmannii*. Shoot weights were not significantly different between the two conifers at the conclusion of the 10-week study.

Relative growth rates (RGR) of the roots were calculated for the entire 10-week growth period while shoot and seedling RGR was computed for the 8-week

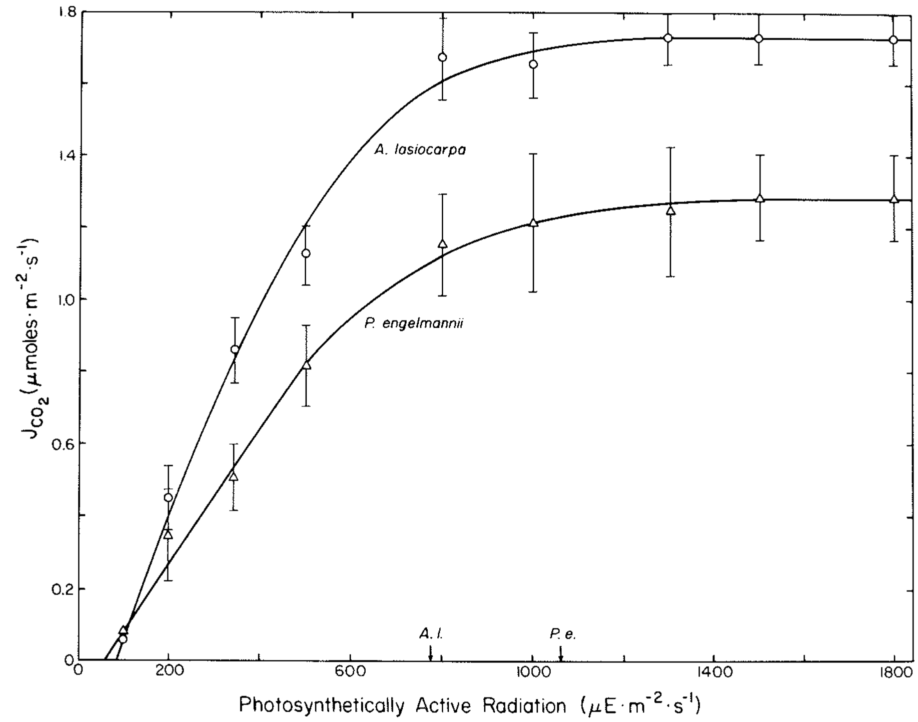

FIG. 2. Response of net photosynthesis (J_{CO_2}) to incident photosynthetically active radiation in 2- to 4-year-old seedlings of *A. lasiocarpa* (*A.l.*) and *P. engelmannii* (*P.e.*). Light saturation of photosynthesis (95% maximum J_{CO_2}) is indicated for each conifer by arrows and vertical bars represent ± 1 standard error of the mean.

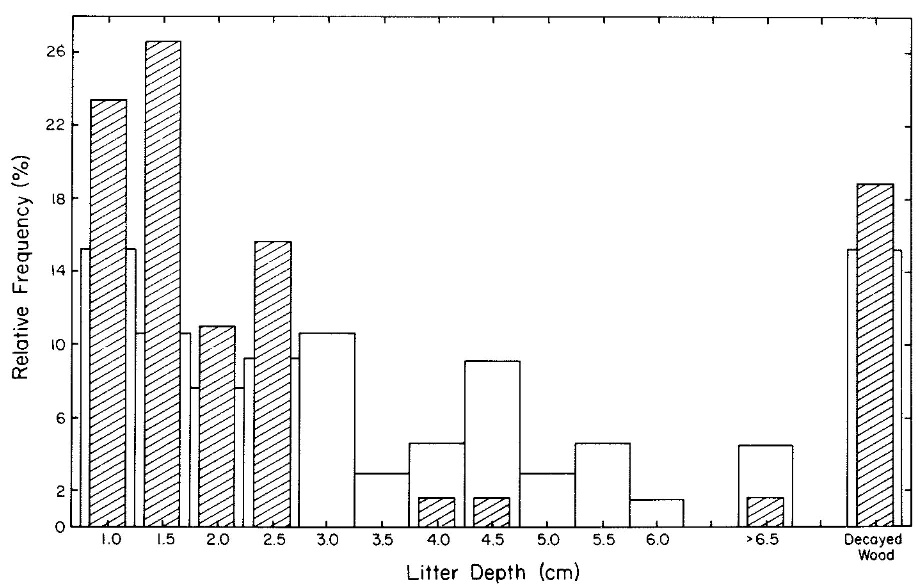

FIG. 3. Relative frequency of seedlings of *A. lasiocarpa* and *P. engelmannii* (combined for the two study sites) according to litter depth (organic matter above mineral soil) and decayed wood. Hatched bars, *P. engelmannii*; open bars, *A. lasiocarpa*.

TABLE 2. Germination characteristics for seeds of *Abies lasiocarpa* and *Picea engelmannii* at constant temperatures

Temperature (°C)	Germination (%)		Time until initial germination (days)		Time until 50% maximum germination (days)	
	P. engelmannii	*A. lasiocarpa*	*P. engelmannii*	*A. lasiocarpa*	*P. engelmannii*	*A. lasiocarpa*
10	3.5(2.1)*	1.0(0.6)*	5	8	7	—
15	40.5(6.8)	7.1(1.4)*	5	7	8	15
20	54.8(6.4)	40.0(2.6)	4	6	5	13
25	42.0(4.5)	46.0(2.9)	5	7	7	15

NOTE: Values in parentheses represent one standard error of the mean.
*Indicates germination is significantly lower than the maximum value ($P < 0.05$).

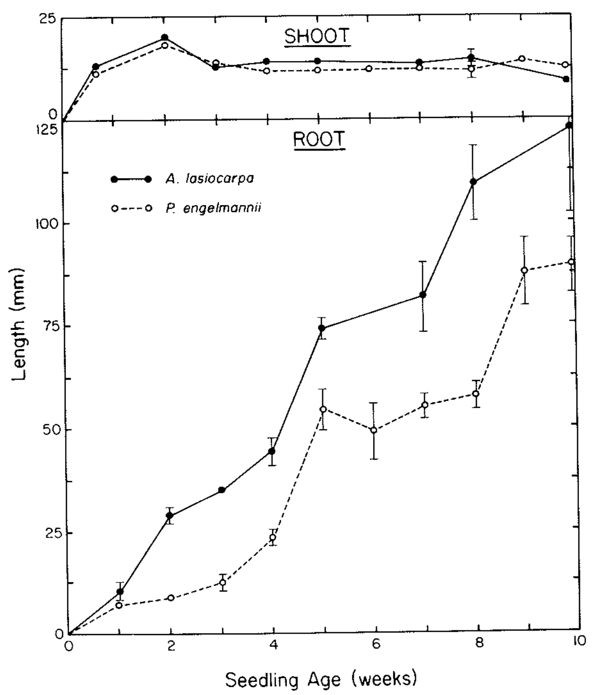

FIG. 4. Root and shoot lengths of seedlings of *A. lasiocarpa* and *P. engelmannii* plotted on a weekly basis for a 10-week period following germination. Vertical bars represent ± 1 standard error of the mean.

TABLE 3. Relative growth rates (grams per gram per day) of entire seedlings and roots and shoots of *A. lasiocarpa* and *P. engelmannii* grown over a 10-week period and harvested at weekly intervals

	P. engelmannii	*A. lasiocarpa*
Seedlings	0.041(0.002)	0.028(0.003)
Shoot	0.038(0.003)	0.019(0.004)
Root	0.051(0.001)	0.055(0.003)
Root/shoot	1.6	2.9

NOTE: Values in parentheses represent one standard error of the mean.

period following the loss of the seed coat (Table 3). Although the RGR of whole seedlings was greater in *P. engelmannii* than in *A. lasiocarpa*, root RGR was greater in *A. lasiocarpa* seedlings. The ratio of root-to-shoot RGR was substantially greater for *A. lasiocarpa* than for *P. engelmannii* seedlings (2.9 vs. 1.6).

Discussion

There were numerous differences between seedlings of *P. engelmannii* and *A. lasiocarpa*. They included understory location, photosynthesis and root growth, and differences in seed size and germination. Seedlings of *A. lasiocarpa* were more abundant in locations receiving less solar radiation (Fig. 1) and had correspondingly greater photosynthetic rates at the lower light levels characteristic of the understory environment (Fig. 2). The smaller seeds of *P. engelmannii* germinated earlier and more rapidly than those of *A. lasiocarpa* and the reduction in germination at lower temperatures was greater for *A. lasiocarpa*. However, root growth and penetration was greater for seedlings of *A. lasiocarpa* (Fig. 4), and they were more abundant at understory locations with thicker litter layers (Fig. 3).

The spatial heterogeneity of understory light in western coniferous forests may be an important factor influencing the location of certain understory species (Young and Smith 1979, 1980). The ability of plants of *A. lasiocarpa* to utilize low light levels more efficiently and the saturation of J_{CO_2} at low incident radiation are characteristic of greater shade adaptation in this species (Boardman 1977; Bazzaz 1979; Young and Smith 1980). However, if low understory light is a factor limiting the abundance of *P. engelmannii* seedlings in the subalpine understory, understory locations receiving quantities of solar radiation below a minimum level should not be occupied by *P. engelmannii* seedlings. No minimum threshold of total daily radiation was apparent for either *P. engelmannii* or *A. lasiocarpa* in the spruce–fir stands studied here (Fig. 1). Therefore, as stand age increases and the canopy closes, the reduced amount of solar radiation reaching the forest floor does not appear to be solely responsible for the lower number of *P. engelmannii* seedlings in the understory relative to those of *A. lasiocarpa*.

Solar radiation striking the forest floor can alter surface temperatures and water relations and, thus, have a strong influence on germination and establishment patterns (Koller 1972). Although *A. lasiocarpa* seedlings were less common in understory locations receiving greater quantities of solar radiation, Knapp and Smith (1981) reported that the water relations of such seedlings did not appear to be adversely affected by exposure to high levels of solar radiation (>30 $MJ \cdot m^{-2} \cdot day^{-1}$). This result sugests that high understory levels of solar radiation ($>10\ MJ \cdot m^{-2} \cdot day^{-1}$) are probably not detrimental to established *A. lasiocarpa* seedlings in the understory. However, the larger seeds of *A. lasiocarpa* were slower to germinate than seeds of *P. engelmannii* and germination was significantly reduced at $\leq 15°C$. These characteristics may delay germination of *A. lasiocarpa* seeds until later in the spring when surface soil moisture is more likely to be limiting and, thus, could decrease germination and establishment of this conifer in microsites that receive greater solar radiation. Rapid germination has been reported to be a potential mechanism for avoiding drought (Wright 1968; Pollock and Roos 1972) and the ability of *P. engelmannii* to germinate rapidly and at low temperatures, demonstrated in the present study and by others (Patten 1963; Kaufmann and Eckard 1977), may allow this conifer to begin establishment earlier in the spring when soil moisture may be more favorable.

Rapid root growth and penetration into the soil may also be important for avoiding drought or temperature extremes (Baker 1972). Many studies indicate that larger seeds produce larger and more vigorous seedlings compared with smaller seeds (Harper and Clatworthy 1963; Pollock and Roos 1972; Schaal 1980). Salisbury (1942) reported that differences in seed size, and consequently differences in seedling growth and root length, may strongly influence successional patterns among species that reproduce solely by seed. Although numerous studies have shown that 1-year-old seedlings of *A. lasiocarpa* have longer roots than similar aged seedlings of *P. engelmannii* (Smith 1955; Eis 1965; Roe et al. 1970; Noble 1973; Day 1964), seed size may influence seedling growth for only a short, but critical period during early establishment (Baker 1972). In the present study, the tap root of *A. lasiocarpa* seedlings was larger and had penetrated deeper into the soil than that of *P. engelmannii* following the initial 2-week period of growth and this difference was maintained throughout the 10-week study. Greater initial root penetration in *A. lasiocarpa* (generated by the larger seed) may increase the probability of successful establishment of this conifer immediately following germination, and the greater ratio of RGR of roots to shoots for *A. lasiocarpa* compared with *P. engelmannii* suggests that a greater proportion of photosynthate may be allocated to root growth in *A. lasiocarpa* during the subsequent period of growth when cotyledons and needles are photosynthesizing.

The different understory patterns observed for *A. lasiocarpa* and *P. engelmannii* may also reflect differences in substrates on the forest floor which are available for establishment. The poor moisture retention of loosely compacted litter is well-known (Smith 1955; Prochnau 1963; Day 1964; Alexander 1974) while decayed wood in the understory has been reported to have excellent moisture retention (Day 1963, 1964). Smith (1954) reported that in mature spruce–fir stands in the northern Rocky Mountains, mineral soil and decayed wood, which occupied 10% of the area, supported 100% of the *P. engelmannii* seedlings. Seedlings of *A. lasiocarpa* were also more abundant on mineral soil and decayed wood; however, 10% were found on litter and moss seedbeds as well. Our results showed that, although the majority of seedlings were found on litter, a larger portion of seedlings of both species also occurred in decomposing wood than would be expected from the area occupied by this substrate (Fig. 3). The more frequent occurrence of *A. lasiocarpa* seedlings on thicker layers of litter suggests that establishment of this species may be less affected by litter depth, possibly due to the greater root penetration measured for seedlings of *A. lasiocarpa*. The detrimental effect of thick litter layers on *P. engelmannii* establishment may be especially severe in old-growth forests since litter depth generally increases with stand age in most forests (Reynolds and Knight 1973; Florence and Lamb 1974; MacLean and Wein 1978).

In summary, the ability of *A. lasiocarpa* to produce significantly longer tap roots may increase the probability of *A. lasiocarpa* establishing on litter layers in the understory of mature spruce–fir forests and, thus, contribute to the greater abundance of this conifer compared with *P. engelmannii* in the understory. However, the presence of decayed wood and small scale variations in forest floor depth may provide a limited number of locations for establishment of *P. engelmannii*, even in very old forests. This feature, coupled with the longer life span of *P. engelmannii* relative to *A. lasiocarpa* and the frequency of fire in this forest type (Day 1972) may allow *P. engelmannii* to remain a codominant climax conifer with *A. lasiocarpa* in the subalpine zone of southeast Wyoming. Low levels of understory light did not appear to be a limiting factor responsible for the lower number of *P. engelmannii* seedlings relative to *A. lasiocarpa*, despite the ability of *A. lasiocarpa* seedlings to photosynthesize more rapidly at low light levels within the understory. Finally, numerous other factors such as seed source availability, type and history of disturbance, aspect, slope, and climatic anomalies may also influence the establishment of these two conifers in the subalpine zone (Day 1964; Romme and Knight 1981). Further studies on the effects and rate of drying in the litter and surface soil layer on seedling growth and survival are needed before the importance of differences in seedling root penetration on the observed distribution patterns of *A. lasiocarpa* and *P. engelmannii* can be evaluated more fully.

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